

This article was downloaded by: [Cornell University]

On: 06 December 2012, At: 17:10

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK

Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:
<http://www.tandfonline.com/loi/ujmp20>

Split Carinae on Tyrannosaurid Teeth and Implications of Their Development

Gregory M. Erickson ^a

^a Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, California, 94720

Version of record first published: 24 Aug 2010.

To cite this article: Gregory M. Erickson (1995): Split Carinae on Tyrannosaurid Teeth and Implications of Their Development, *Journal of Vertebrate Paleontology*, 15:2, 268-274

To link to this article: <http://dx.doi.org/10.1080/02724634.1995.10011229>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.



SPLIT CARINA ON TYRANNOSAURID TEETH AND IMPLICATIONS OF THEIR DEVELOPMENT

GREGORY M. ERICKSON

Department of Integrative Biology and Museum of Paleontology,
University of California, Berkeley, California 94720

ABSTRACT—Examination of hundreds of shed and intact tyrannosaurid teeth from several taxa and formations revealed that the presence of split carinae is widespread. Approximately 11% of the surveyed teeth showed some degree of expression of this trait. Split carinae were found in *Tyrannosaurus rex*, *Daspletosaurus* sp., *Albertosaurus* sp., and *Alectrosaurus olsoni*. The trait is also found in non-tyrannosaurids (e.g., *Allosaurus fragilis*). Trauma, aberrant tooth replacement, or genetic factors may have led to the development of split carinae, although the latter finds the most support. If the split carinae are caused by genetic factors, they may prove valuable in assessing the dispersion patterns and evolution of the tyrannosaurids.

INTRODUCTION

In the summer of 1987 an unusual tyrannosaurid lateral tooth crown (maxillary or dentary tooth) was unearthed by a crew from the University of California, Museum of Paleontology (UCMP) and the University of Alaska Museum (UAM) from upper Cretaceous sediments on the North Slope of Alaska. Its carina (or serration row) has the unusual feature of an anterior basal split or fork (Fig. 1A). In a normal tyrannosaurid tooth a single carina runs midsagittally along the anterior and posterior edges of the tooth crown. Hundreds of isolated Late Cretaceous tyrannosaurid teeth and several intact dentitions were examined to document further instances of this trait. To provide a comparative base, large theropod teeth of non-tyrannosaurid taxa were examined as were intact teeth of *Varanus komodoensis*, a large predaceous lizard with recurved, serrated teeth superficially similar to those of theropod dinosaurs. This investigation revealed the frequency and character of split carinae in tyrannosaurids as well as their geographic and stratigraphic variability. Similar features were found in other taxa with serrated teeth. A hypothesis for the cause of the tooth anomalies is presented. Prior to this investigation, Bohlin (1953) documented a split carina in a large theropod from the Minhe Formation of China. Also, Farlow et al. (1991) observed split carinae in lateral teeth of tyrannosaurids (Currie and Farlow, pers. comm.).

MATERIAL AND METHODS

Approximately sixteen hundred individual tyrannosaurid teeth from Cretaceous sediments of the Judith River, Two Medicine, and Hell Creek formations of Montana; the Judith River, Horseshoe Canyon, and Wapiti formations of Alberta; and the Prince Creek Formation of Alaska were examined. (Eberth and

Hamblin, 1993, have recommended that the Judith River Formation, sensu McLean [1971], be raised to group status; however, the former designation is retained in this paper.) The teeth are housed in the Museum of the Rockies (MOR, Bozeman), the Royal Tyrrell Museum of Palaeontology (RTMP, Drumheller), the University of California Museum of Paleontology (UCMP, Berkeley) and the University of Alaska Museum (UAM, Fairbanks), (see Table 1). The teeth from formations other than the Hell Creek were shed by *Albertosaurus* and/or *Daspletosaurus*. (It should be noted that there is debate as to the number of valid tyrannosaur taxa and none is distinguishable solely based on isolated teeth). The possibility exists that the rare tyrannosaurid, *Aublysodon mirandus*, was represented by some of the smaller teeth; however, its diagnostic premaxillary teeth were excluded due to the uncertainty of this taxon's validity and taxonomic affinities. The teeth from the Hell Creek Formation were predominantly from *Tyrannosaurus rex*. Possibly a few teeth from *Aublysodon* and/or *Nanotyrannus lancensis*, which are both small and rare taxa, were included. (*Albertosaurus lancensis*/*Albertosaurus megagracilis* = *Tyrannosaurus rex*; unpubl. data). Less than 5% of the teeth surveyed were from the size ranges to which these smaller taxa overlap, so their possible influence on the split carinae frequencies was probably negligible.

Each tooth was examined for carina splits (see Fig. 1A, B). If a split was located, development of serrations and wear patterns were noted. Many teeth were broken or poorly preserved and hundreds of teeth were deemed unsuitable for proper evaluation. The tabulated specimens ($n = 993$) were restricted to internal teeth with the basal ends of the serration rows intact and premaxillary teeth with the greater part of their coronal end preserved, the usual locations of their respective splits (Fig. 1A, B).

In order to determine if split carinae are present

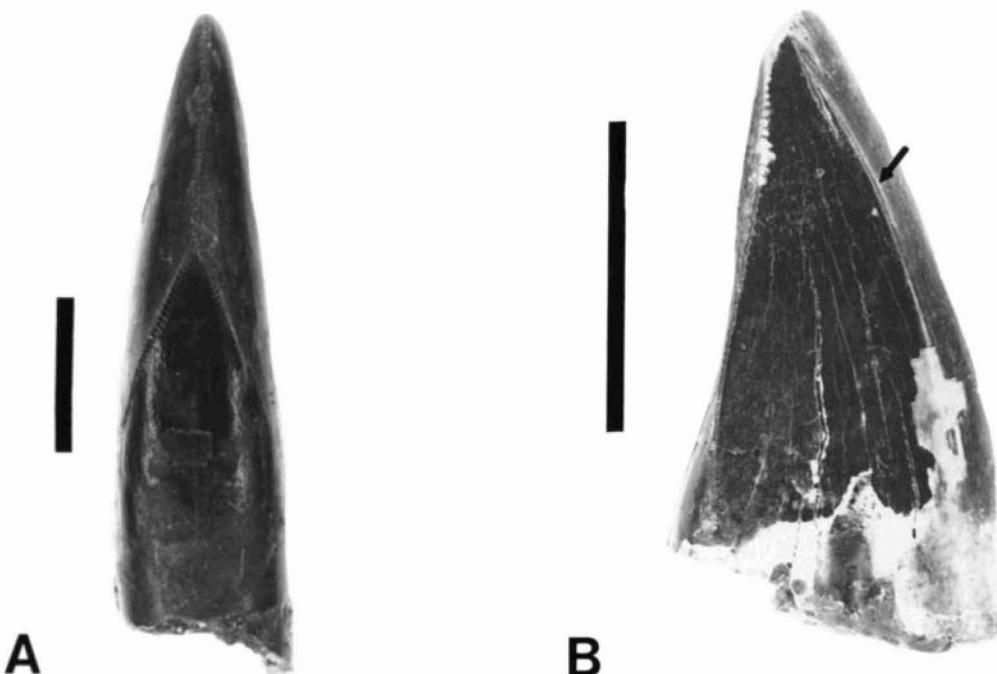


FIGURE 1. **A**, Tyrannosaur tooth (UAM-AK83.V90) from the Prince Creek Formation of Alaska bearing a split anterior carina. **B**, Tyrannosaur premaxillary tooth (RTMP-P81.31.59) from the Horseshoe Canyon Formation of Alberta (Canada) bearing a split carina. Arrow denotes an accessory carina segment on the anterolateral face of the tooth. Scale bars equal 1 cm.

throughout all tooth positions in affected individuals, teeth from tyrannosaurid jaws were surveyed for the trait. When such instances were subsequently found, CT-scanning was employed to see if the replacement teeth were similarly afflicted. To establish if the split carinae trait occurs in other taxa bearing serrated teeth, non-tyrannosaurid large theropod (from RTMP, MOR) and *Varanus komodoensis* (from the University of California Museum of Vertebrate Zoology, UCMVZ) teeth were surveyed (see Table 2).

RESULTS

Approximately 11% (114 out of 993) of the tyrannosaurid teeth examined showed the split carinae trait. The trait showed graded degrees of expression (*sensu* Harris and Bailit, 1980), ranging from well-developed carina forks with high relief and serrations on both segments (Fig. 1A), to splits with one segment serrated and the other showing a low-relief unserrated keel barely visible to the naked eye. The splits were almost

TABLE 1. Tabulation of split carinae phenomenon in North American tyrannosaurids.

Formation	Stage	Locality (institution)	% split lateral teeth	% split premax. teeth	Total anomaly percentage	Forma- tional anomaly percentage
Judith River	Campanian	Montana (MOR)	9.7 (3/31)	0.0 (0/17)	6.25 (3/48)	
Judith River	Campanian	Alberta (RTMP)	9.4 (32/339)	12.8 (10/78)	10.1 (42/417)	9.7
Two Medicine	Campanian	Montana (MOR)	10.6 (33/310)	18.8 (3/16)	11.0 (36/326)	11.0
Horseshoe Canyon*	e. Maastrich.	Alberta (RTMP)	24.3 (18/74)	50.0 (5/10)	27.4 (23/84)	27.4
Prince Creek	e. Maastrich.	AK (UCMP/UAM)	29.0 (6/21)	0.0 (0/2)	26.0 (6/23)	26.1
Hell Creek	lt. Maastrich.	Montana (MOR)	0.0 (0/24)	0.0 (0/3)	0.0 (0/27)	
Hell Creek	lt. Maastrich.	Montana (UCMP)	8.0 (4/50)	0.0 (0/5)	7.3 (4/55)	
Hell Creek	lt. Maastrich.	Montana (RTMP)	0.0 (0/13)	—	0.0 (0/13)	4.2
Total percentage (all formations)	—	—	11.1 (96/862)	13.7 (18/131)	11.4 (114/993)	—

*This sample includes specimens from the Wapiti Formation as well.

TABLE 2. Tabulation of non-tyrannosaurid taxa examined for split serration rows.

Taxon	Locality (institution)	Number of maxillary teeth examined	Number of premaxillary teeth examined	Number of anomalies observed
<i>Varanus komodoensis</i>	UCMVZ	74	6	0
<i>Torvosaurus tanneri</i>	RTMP	2	—	0
<i>Allosaurus fragilis</i>	RTMP, MOR	27	—	0
<i>Yangchuanosaurus</i> sp.	RTMP	4	—	0
Totals	—	107	6	0

invariably on the anterior aspect of the teeth. Wear was found predominantly on only one of the split carina segments, which is presumably the normal segment (located on the lingual side of nonsplit teeth). The lack of wear on the accessory labial carina segments suggests no functional significance of the split carina trait.

The lateral and premaxillary teeth showed similar ratios of split carinae: 11.1% (96/862) and 13.7% (18/131), respectively (not statistically different at the 0.05 level by a z-test for proportions).

The oldest surveyed albertosaurs (*Albertosaurus/Daspletosaurus*) from the upland Campanian Two Medicine Formation had split carinae in 11.0% of the sampled teeth. The adjacent lowland Judith River Formation, which was initially deposited as the Claggett Sea regressed to the east, showed a 9.7% split carinae frequency. (The two respective frequencies are not statistically different at the 0.05 level by a z-test for proportions.) The younger lower Maastrichtian Prince Creek and Horseshoe Canyon/Wapiti formations which were deposited following the Bear Paw Sea's regression had split carinae in 26.1% and 27.4% of the surveyed teeth, respectively (not statistically different at the 0.05 level by a z-test for proportions). The youngest teeth surveyed (from *Tyrannosaurus rex*) came from the Maastrichtian Hell Creek Formation, which was deposited after the Bearpaw Sea had further regressed. These teeth had splits in only 4.2% of the sample.

Two instances of teeth with split carinae preserved in the jaws of tyrannosaurids were located. In a left dentary of *Albertosaurus* sp. (BYU 9398) from the Kaiparowits Formation of Utah, the fourth dentary tooth has a serrated split anterior carina. The third tooth may also bear an unserrated split carina but is too poorly preserved to be certain. The other two teeth in this specimen appear to be normal. The second specimen with a defect is an albertosaur (*Daspletosaurus* sp., MOR 590), from the Two Medicine Formation of Montana. Among the associated teeth undeniably belonging to this animal was a split but unserrated lateral tooth (the 18 other surveyed teeth were not split). It was not possible via CT-scanning to determine if the split carinae trait is present in all replacement teeth at each affected position. However, these findings show that split carinae show localized expression (i.e., the

trait is not expressed at every tooth position in a tyrannosaur's dentition).

Examination of non-tyrannosaurid taxa with serrated teeth did not reveal any analogous tooth defects (Table 2). However, Carpenter has reported a tooth of *Allosaurus fragilis* with a split carina (pers. comm.). This finding shows that the split carinae anomaly is not restricted to tyrannosaurids.

DISCUSSION

In light of the findings from this survey, it appears that tyrannosaurid teeth with split carinae are common with frequencies exceeding 25% in some formations (Table 1).

The cause of this trait is not immediately apparent. An unfortunate lack of studies on tooth malformities in reptilian taxa forces one to seek analogies in extant mammalian taxa (primarily humans) in order to explain their expression. If we assume that the developmental pathways involved in tooth production in vertebrates are conservative, then the causes of dental anomalies may be comparable between reptiles and mammals. In support of such reasoning are the findings of Ferguson (1981), who has shown that many human cranial malformities and their causes can be studied using crocodilians. Additionally, reptiles occasionally possess teeth with supernumerary cusps (e.g., *Alligator mississippiensis*, pers. obs.; *Tyrannosaurus rex*, Currie, pers. comm.), a defect pervasive in many mammalian taxa.

Various human tooth deformities have been linked to monogenic and polygenic expression, gender, nutrition, trauma, race, aberrant replacement, and other factors (reviewed by Hillson, 1986). Given the available data set, three of the more plausible and testable of these causes, trauma, aberrant replacement, and genetic polymorphisms, were investigated and the evidence is presented below.

Given that tyrannosaurids were probably aggressive predators, trauma may have caused the formation of their split carinae. Research on extant taxa has shown that dental trauma can affect tooth morphology (Colyer, 1936; Reif, 1980; see Hillson, 1986) and incidences of dental trauma have been noted in various tyrannosaurids (Molnar, 1973; McGinnis, 1982; Mol-

nar and Farlow, 1990). The finding of greater proportions of split carinae in the gracile-jawed albertosaurs versus the more robust-jawed *Tyrannosaurus rex* would seem to support a traumatic causality (Table 1). However, much of the data seems inconsistent with that which would be expected if trauma caused the split carinae. For instance, the consistent structure and location of the split carinae is problematic, as most trauma-related dental deformities in extant taxa are variable in form (e.g., Colyer, 1936). One might have expected to find wound calluses on jaw bones bearing the split teeth, but both dentaries possessing split carina teeth have a normal (non-pathological) bone texture (although bone calluses can disappear in time with bone remodeling). The relatively high frequency of split carinae in tyrannosaurids does not seem consistent with much rarer (<1%) trauma-induced defects expressed in crocodilians which often suffer dental injuries (unpubl. data). Additionally, if trauma was the cause of the anomalies, one might have expected statistical variability between the smaller and functionally differing premaxillary teeth versus the lateral teeth. Finally, if trauma was the principal cause, it would be necessary to explain why the Campanian albertosaurs and the early Maastrichtian albertosaurs have such large differences in anomaly incidence rates (~10% vs. ~27%; Table 1) even though they are considered equivalent in size (and perhaps are the same species). A change in diet to more aggressive prey types could be inferred for early Maastrichtian times. However, the prey species of the upland and lowland Campanian faunas (Two Medicine and Judith River formations, respectively) probably differed significantly (see Brinkman, 1990). Yet nearly equivalent anomaly percentages (~10%) are found between these upland and lowland Campanian tyrannosaurids.

Another hypothesized cause for the split carinae trait was aberrant tooth replacements. The continued tooth eruptions in tyrannosaurids, due to their possession of a polyphyodont dentition, may have made them prone to frequent mishaps, particularly in light of the extreme degree of bone and soft tissue remodeling that such a system requires. An analogy may be made with proboscians which effectively have a multiple tooth replacement mechanism (a total of six teeth erupt sequentially and continuously throughout life) where significant alveolar bone reconstruction renders them more prone to dental developmental mishaps than most other mammalian taxa (Roth, 1989). Alligators, which also show substantial remodelling associated with tooth turnover, occasionally show unusual tooth replacements such as paired functional teeth and supernumerary teeth (unpubl. data). However there are problems with this hypothesis, such as the rarity of tooth deformities in alligators (<1%; unpubl. data). Additionally, the consistent morphology and location on individual teeth, graded development, and temporal and geographic consistencies of the split carinae do not support an aberrant tooth replacement hypothesis.

A third tenable hypothesis is that the tyrannosaurid

split carinae had a genetic derivation (i.e., the trait is a genetic polymorphism). Multigenically expressed secondary tooth traits (*sensu* Turner, 1989) or anomalies have been extensively studied in both extant and fossil mammalian taxa (Barnosky, 1986, 1993; Greenberg et al., 1986; Turner, 1986, 1987, 1989; Turner et al., 1991). Similarities between these mammalian dental studies and the tyrannosaurid split carinae data provide some support for a multigenetic cause of this trait. Important similarities are outlined below:

Mammalian genetic tooth traits show graded degrees of expression (Barnosky, 1986, 1993; Turner, 1987; Turner et al., 1991) as does the split carinae trait in tyrannosaurids.

Mammalian secondary tooth traits are found at the same location on affected teeth (e.g., the “accessory cusp” on *Cupidinimus* P4 is always on the protoloph; Barnosky, 1986; extra carinae associated with “shoveling trait” on human incisors and canines are always in a lingual and marginal location; Turner et al., 1991). Split carinae are almost invariably located on the anterior basal thirds of lateral teeth and apical thirds of premaxillary teeth (Fig. 1A, B).

Mammalian secondary tooth traits are phenotypically neutral with no apparent selective significance (Barnosky, 1986, 1993; Turner, 1987, 1989). A lack of wear on secondary tooth traits or rapid loss of these traits with use has been used as evidence to support this assertion. The accessory carina segments on split carina tyrannosaur teeth similarly show no wear patterns, implying neutrality for the trait.

Mammalian secondary tooth traits are usually locally expressed within dentitions (e.g., in *Homo*, “canine mesial ridges” are only found in upper canines; “shoveling trait” is found only in upper and lower incisors and canines; “radical trait” can be found on any tooth’s root but is generally not expressed in every tooth in an individual’s dentition; Turner et al., 1991). These findings complement the research of Baily (1985), who showed that rodents have many genes with overlapping fields of morphological control in the jaw bones that act locally in developing each tooth or groups of adjacent teeth. The discovery of split carinae on individual teeth from intact tyrannosaurid dentitions shows that this trait is also locally expressed.

Mammalian secondary tooth traits can involve carinae (albeit unserrated) that superficially resemble tyrannosaurid extra carinae (e.g., in *Homo* “canine distal accessory ridges” and the lingual ridges associated with “shoveling”; see Hrdlicka, 1920; Hillson, 1986). These extra carinae involve both enamel and dentine in their formation and have a general longitudinal trend like the split carinae in tyrannosaurs. This shows that the formation of extra carinae is within the realm of morphologies that can be produced as genetically controlled secondary tooth traits.

Mammalian secondary tooth traits have frequencies of expression that typify the demes from respective regions (e.g., Great Plains species of *Cupidinimus* have >50% frequencies of “accessory premolar cusps”;

Barnosky, 1986). The consistent 10% frequency of split carinae in Campanian albertosaurs from the adjacent Two Medicine (northern Montana) and Judith River (northern Montana and southern Alberta) formations could be explained by gene pool sharing (Table 1). The high frequency (27%) of split carinae teeth in the Horseshoe Canyon Formation of Alberta and Prince Creek Formation of Alaska may also be due to sampling from the same gene pool (Table 1). (I am not implying that the tyrannosaurid tooth samples from each formation represent sampling from separate ecological demes because it is possible that these samples included individuals from more than one tyrannosaur species. However gene pool sharing may still have occurred in these tyrannosaurs at higher taxonomic levels [i.e., interspecifically] due to common descent. Two closely related species of tyrannosaur may have shared the same frequencies of split carinae genes if during their divergence from one another [cladogenesis] these genes were unaltered. Such gene pool sharing would explain the patterns that the tyrannosaur split carinae data and the mammalian secondary tooth characteristics have in common.)

Mammalian secondary tooth traits are not expressed in every individual in a deme (Barnosky, 1986). The varying formational frequencies showing the split carinae trait and the finding that only several individual tyrannosaurids had split carinae expressed in intact dentitions seems consistent with these findings.

The frequencies for mammalian secondary tooth traits range from 0–100% within demes (e.g., Barnosky, 1986). Therefore, trait frequencies exceeding 25% for tyrannosaurs from some formations (e.g., Horseshoe Canyon Formation; Table 1) would not be unexpected if the split carinae trait had a genetic derivation.

Mammalian secondary tooth traits show temporal stability (e.g., in *Cupidinimus*, >80% frequencies of “accessory cusps” on P4 only occur during the Barstovian; Barnosky, 1986). The Campanian percentages of split carinae in tyrannosaurids from Montana and Alberta showed a consistency of 10% during the five-million-year interval surveyed. The early Maastrichtian tyrannosaurids from Alberta and Alaska showed a 27% frequency of expression over approximately a four-million-year interval. A four-percent frequency of split carinae appears to typify the latest Maastrichtian Hell Creek Formation tyrannosaurids, which spans roughly six million years in the Montana survey area.

Mammalian secondary tooth trait frequencies do not show clinal variability (Barnosky, 1986, 1993; Greenberg et al., 1986; Turner, 1986, 1987, 1989). There is comparable evidence from the tyrannosaurid split carinae data. The oldest tyrannosaurids from this survey are found 80 mybp in the Two Medicine Formation highlands. During this time these tyrannosaurids were confined by the Claggett Sea to a strip along the eastern flank of the Rocky Mountains in Montana and Alberta. The Claggett Sea then gradually regressed to the east and exposed the Judith River lowlands, which these

tyrannosaurids undoubtedly came to inhabit. The fact that the 10% split carinae frequency is found in both the highland and lowland environments suggests no clinal variability for the split carinae trait (Table 1). Perhaps even stronger evidence is found with the 27% consistency between the Horseshoe Canyon Formation of Southern Alberta and the Prince Creek Formation of Alaska. The environments certainly differed greatly between these two areas (e.g., Clemens and Nelms, 1993), particularly in climatic terms, and yet there appears to be no variability in the expression of split carinae between these vastly separated tyrannosaurids (Table 1).

Mammalian secondary tooth traits change due to genetic drift (Barnosky, 1986, 1993; Greenberg et al., 1986; Turner, 1987, 1989). The split carinae data for tyrannosaurids shows temporal consistencies, during the Campanian, early Maastrichtian, and late Maastrichtian (Table 1). However, there were changes in frequencies between these times. The change between the Campanian and early Maastrichtian may be due to the population bottleneck (Bakker, 1977; Horner, 1984; Horner et al., 1992) caused by the Bearpaw Sea transgression. This major transgression submerged 98% of the local terrestrial realm along the Western Interior (Gill and Cobban, 1966) and must have caused a reduction in the number of tyrannosaurids that the region could support. This gene pool reduction may have randomly influenced a shift in the frequency of the split carina trait from 10% (Campanian) to 27% (early Maastrichtian).

Closely related species of mammals show differing frequencies of secondary tooth traits which can be used as genetic signatures to diagnose taxa (Barnosky, 1986). The albertosaurs (*Albertosaurus/Daspletosaurus*) from the early Maastrichtian are morphologically distinct from *T. rex* from the late Maastrichtian. The frequencies of ~27% and ~4.0% of split carinae from these respective stages may reflect these taxonomic differences.

It should be noted that although some non-tyrannosaurids (e.g., *Allosaurus fragilis*) have split carinae, this does not detract from a genetic argument as the cause of split carinae. Primates besides *Homo* are known to have the “shoveling trait” (Hrdlicka, 1920), which is also presumed to have a genetic cause. This example suggests that the genes causing tooth malformities may be conserved in related lineages by common descent (in this case within the primates). The tyrannosaur/allosaur possession of split carinae may similarly reflect their common tetanurine ancestry (see Gauthier, 1986). The control of tooth development by multigenic influences is likely a potential that is shared by mammals and reptiles due to their common descent as amniotes. More subtle influences on individual tooth form (such as specific cusp number, size, form, and location) are clearly separate derived traits unique to each lineage.

Of the hypotheses which were considered as possible

causes of the split carinae trait: trauma, aberrant replacement of teeth, and genetic polymorphism, the latter seems to find the most support. However, the data is certainly not conclusive and as noted above, there are other causes of tooth abnormalities that are currently untestable on dinosaur taxa (e.g., nutritionally induced anomalies). Further testing of the genetic polymorphism hypothesis seems warranted and perhaps should be directed toward tyrannosaurs from temporally equivalent formations to those examined in this study. For example, if the Campanian albertosaurs from Montana and Alberta had a range extending into more southerly states (e.g., in the Kaiparowits Formation of Utah), then it would be predicted that the split carinae trait would similarly be expressed in ~10% of the teeth from these regions (this assumes that the environmental trigger for their expression was equable). It would also be interesting to survey *T. rex* teeth from the southern portion of the Western Interior (e.g., McRae Formation of New Mexico) and from more northerly sediments (e.g., Scollard Formation of Alberta) to see if the trait frequencies differ from the ~4% frequency of Montana. Another possible test of a genetic cause for the formation of split carinae would be to survey the teeth of *Alectrosaurus olseni* or *Allosaurus fragilis* (Currie and Carpenter both have mentioned that these taxa show split carinae: pers. comm.) to see if similar patterns to those found in this study are observed.

Unfortunately the taxonomy of the Tyrannosauridae is in disarray and is under revision (Currie et al., 1990). If the tyrannosaurid split carina trait proves to have a multigenic derivation and the taxonomy of the Tyrannosauridae is resolved, then tracing of the evolution and migrational patterns in tyrannosaurs may ultimately be possible. This has been done for prehistoric mammals using secondary tooth traits with spectacular results (Barnosky, 1986, 1993; Greenberg et al., 1986; Turner, 1986, 1987, 1989; Turner et al., 1991).

ACKNOWLEDGMENTS

I thank Philip Currie, John Horner, Gayle Nelms, Kevin Padian, Bill Clemens, Jim Farlow, Tony Barnosky, Jim Patton, Tom Holtz, Brooks Britt, Darren Tanke, Scott Sampson, Mark Goodwin, Chris Bell, Ray Rogers, Mike Shapiro, Elaine Nissen, and David Varricchio for helpful advice. I also am grateful to the museum and staff of each of the museums where specimens were provided for examination: the Royal Tyrrell Museum of Palaeontology, the Museum of the Rockies, the University of California Museum of Paleontology, the University of Alaska Museum, and the University of California Museum of Vertebrate Zoology. Special thanks go to Katie Best and the Bozeman Deaconess Hospital for providing CT-scanning assistance and Chris Genovese and Mary Sara McPeek for statistical help. Funding for this project was provided

by a John D. and Catherine T. MacArthur Foundation Fellowship awarded to John R. Horner, and a travel grant provided by the Department of Integrative Biology (University of California, Berkeley).

LITERATURE CITED

- Baily, D. W. 1985. Genes that effect morphogenesis of the murine mandible: congenic strain analysis. *Journal of Heredity* 76:107–114.
- Bakker, R. T. 1977. Cycles of diversity and extinction: a plate tectonic topographical model; pp. 431–478 in A. Hallam (ed.), *Patterns of Evolution*. Elsevier, Amsterdam.
- Barnosky, A. D. 1986. New species of the Miocene rodent *Cupidinimus* (heteromyidae) and some evolutionary relationships within the genus. *Journal of Vertebrate Paleontology* 6:46–64.
- . 1993. Mosaic evolution at the population level in *Microtus pennsylvanicus*; pp. 24–59 in R. A. Martin and A. D. Barnosky (eds.), *Morphological Change in Quaternary Mammals of North America*. Cambridge Press, Cambridge.
- Bohlin, B. 1953. Fossil reptiles of Mongolia and Kansu. Sino-Swedish Expedition, Publication 37:1–113.
- Brinkman, D. B. 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 78:37–54.
- Clemens, W. A., and L. G. Nelms. 1993. Paleoecological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. *Geology* 21:503–506.
- Colyer, F. 1936. *Variations and Diseases in the Teeth of Animals*. John Bale, Sons and Danielson, London, 750 pp.
- Currie, P. J., J. K. Rigby, Jr., and R. E. Sloan. 1990. Theropod teeth from the Judith River Formation of Southern Alberta, Canada; pp. 107–125 in P. J. Currie and K. Carpenter (eds.), *Dinosaur Systematics*. Cambridge University Press, Cambridge.
- Eberth, D. A., and A. P. Hamblin. 1993. Tectonic, stratigraphic, and sedimentologic significance of a regional discontinuity in the upper Judith River Group (Belly River wedge) of southern Alberta, Saskatchewan, and northern Montana. *Canadian Journal of Earth Sciences* 30:174–200.
- Farlow, J. O., D. L. Brinkman, W. L. Abler, and P. J. Currie. 1991. Size, shape and serration density of theropod dinosaur lateral teeth. *Modern Geology* 16:161–198.
- Ferguson, M. W. J. 1981. The value of the American alligator (*Alligator mississippiensis*) as a model for research in craniofacial development. *Journal of Craniofacial Genetics and Developmental Biology* 1:123–144.
- Gauthier, J. A. 1986. A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, University of California, Berkeley, 564 pp.
- Gill, J. R., and W. A. Cobban. 1966. The Red Bird section of the Upper Cretaceous Pierre Shale, Wyoming. U.S. Geological Survey Professional Paper 393A:1–69.
- Greenberg, J. H., C. G. Turner II, and S. L. Zegura. 1986. The settlement of the Americas: a comparison of the

- linguistic, dental, and genetic evidence. *Current Anthropology* 27:477–497.
- Harris, E. F., and H. L. Bailit. 1980. The metaconule: a morphological and familial analysis of a molar cusp in humans. *American Journal of Physical Anthropology* 53:349–358.
- Hillson, S. 1986. *Teeth*. Cambridge University Press, Cambridge, 376 pp.
- Horner, J. R. 1984. Three ecologically distinct vertebrate faunal communities from the Late Cretaceous Two Medicine Formation of Montana with discussion of evolutionary pressures induced by interior seaway fluctuations; pp. 299–303 in J. D. McBane and P. B. Garrison (eds.), *Montana Geological Society Field Conference Guidebook*. Montana Geological Society, Billings.
- , D. V. Varricchio, and M. B. Goodwin. 1992. Marine transgressions and the evolution of Cretaceous dinosaurs. *Nature* 358:58–61.
- Hotton, N., III. 1980. An alternative to dinosaur endothermy, the happy wanderers; pp. 311–350 in R. D. K. Thomas and E. C. Olsen (eds.), *A Cold Look at the Warm Blooded Dinosaurs*. AAAS Selected Symposia Series 28. Westview Press, Boulder.
- Hrdlicka, A. 1920. Shovel shaped teeth. *American Journal of Physical Anthropology* 3:429–465.
- McGinnis, H. J. 1982. Carnegie's Dinosaurs. The Board of Trustees, Carnegie Institute, Pittsburgh, 119 pp.
- McLean, J. R. 1971. Stratigraphy of the Upper Cretaceous Judith River Formation in the Canadian Great Plains. Saskatchewan Research Council, Geology Division, Report 11.
- Molnar, R. E. 1973. The cranial morphology and mechanics of *Tyrannosaurus rex* (Reptilia: Saurischia). Ph.D. dissertation, University of California, Los Angeles, 450 pp.
- , and J. O. Farlow. 1990. Carnosaur paleobiology; pp. 210–224 in D. B. Weishampel, P. Dodson, and H. Osmolska (eds.), *The Dinosauria*. University of California Press, Berkeley, California.
- Reif, W. E. 1980. A mechanism for tooth pattern reversal in sharks: the polarity switch model. *Roux's Archives of Developmental Biology* 188:115–122.
- Roth, V. L. 1989. Fabrication noise in elephant dentitions. *Paleobiology* 15:165–179.
- Turner, C. G., II. 1986. Dentochronological separation estimates for the Pacific Rim populations. *Science* 232: 1140–1142.
- . 1987. Late Pleistocene and Holocene population history of East Asia based on dental variation. *American Journal of Physical Anthropology* 73:305–321.
- . 1989. Teeth and prehistory in Asia. *Scientific American* 260:88–96.
- , C. R. Nichol, and G. R. Scott. 1991. Scoring procedures for key morphological traits of the permanent dentition: the Arizona State dental anthropology system; pp. 13–32 in M. A. Kelley and S. L. Clark (eds.), *Advances in Dental Anthropology*. Wiley-Liss, New York.

Received 14 June 1993; accepted 17 January 1994.